



Mechanisms of species coexistence in a lawn community: mutual corroboration between two independent assembly rules

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Abstract: Assembly rules are measures of community structure that link observed patterns with ecological processes, and as such may help to elucidate the mechanisms by which species coexist. We apply two approaches to a lawn community – limiting similarity and guild proportionality – hoping that agreement between them might give robust conclusions. We tested for agreement between these two assembly rules using functional characters that are related to two aspects of species function – light capture and response to defoliation.

We combined point quadrat data and a null model approach to test for limiting similarity – a tendency for species differing in functional characters to co-occur more often than expected at random – in turves extracted from the lawn community. Examining the variance in the characters of the species co-occurring at each point, evidence for limiting similarity was found for mowing removal (the proportion of leaf area removed in mowing events). There was greater variation between the species co-occurring at a point than expected at random (i.e., under an appropriate null model). However, no such evidence was found for characters related uniquely to light capture, such as specific leaf area and pigment concentrations.

In a previous study in the same community, “intrinsic” guilds had been determined from co-occurrences within the lawn community and from a competition experiment, as those effective in determining species assembly and co-existence. These intrinsic guilds are shown by *t*-test to differ in the proportion of their biomass removed in mowing (MRI), which is of course related to the height at which their leaf area is held. However, again no differences were seen in characters related uniquely to light capture.

Thus, the two different approaches to assembly rules – guild proportionality and limiting similarity – agree that differences in response to mowing are responsible for species co-existence in the lawn community. The agreement between these two approaches, tested on independent datasets of quite different type from the same community, gives possibly the strongest evidence so far that niche differentiation may be responsible for local co-existence in plant communities. However, although MRI is related to this co-existence the lack of correlation with light-capture characters leads to speculation that the effects might be via the below-ground behaviour of the species.

Abbreviation: MRI – Mowing Removal Index.

Nomenclature: as in Wilson and Roxburgh (1994).

Introduction

Species co-existence by differentiation in resource use is well established in ecological theory (MacArthur and Levins 1967). Assembly rules, by linking observed community patterns to ecological processes such as competition, allow mechanisms of coexistence to be tested without the drawbacks of disturbing the community that

are inherent to experimental approaches (Wilson 1999a). We can have special confidence in the reality of assembly rules when there is agreement between different types of rule. Most studies have concentrated on searching for patterns rather than considering whether the functional characters measured relate to the niche axes that dictate the strength of competition between species (e.g., Bycroft et

al. 1993, Wilson et al. 1996, Weiher et al. 1998, Mucina and Bartha 1999, Brown et al. 2000). Agreement between assembly rules that are based on functional characters would increase our ability to hypothesize the mechanisms of plant species coexistence. Here, we use two assembly rules approaches – limiting similarity and guild proportionality – to test whether alpha niche differentiation (i.e., differentiation in resource use and acquisition, Wilson 1999b) is responsible for the previously-demonstrated coexistence in a lawn community.

Limiting similarity

MacArthur and Levins' (1967) theory of limiting similarity suggests that there is a limit to how similar species can be in their resource requirements and still co-exist – if a pair of species are too similar, one will be competitively excluded. MacArthur and Levins considered, for theoretical convenience, one niche axis. We can use more axes, but since we cannot know the species' exact resource requirements, we have to use species functional characters (e.g., specific leaf area) as proxies (e.g., Parish and Bazzaz 1976, Armbruster et al. 1994, Weiher et al. 1998). We examine here characters that are expected to be related to two aspects of the survival of plant species in a lawn – susceptibility to defoliation and light harvesting. Evidence for MacArthur and Levins' theory would be for co-occurring species to differ more in the measured characters than expected at random. Limiting similarity might occur either in alpha-niche (i.e., types of resources used) or beta-niche (i.e., type of environment occupied) space, but as our study deals with a single community in a homogenous environment we consider only alpha-niche characters.

Intrinsic Guilds

For our study community, an assembly rule has already been established that is based on guild-proportionality, i.e., a tendency for there to be a relatively constant representation of different guilds at a point. Guild proportionality assumes that guilds differ in their alpha-niche (i.e., the types of resources they use), so that a species may invade sites that are dominated by species from another guild, since there will be resources free for it to use (Wilson 1989). Guilds are usually formed *a priori* on the basis of morphology and/or taxonomy (Wilson 1999b), but this type of approach has been criticised since the assumption that these criteria are the ecologically relevant ones is usually not tested (de Kroon and Olff 1995). To avoid this problem, Wilson and Roxburgh (1994) grouped species from the Botany Lawn community at the Uni-

versity of Otago into "intrinsic" guilds on the basis of their co-occurrence at points within the community, allocating species to guilds to maximize constancy in guild proportions. Thus, species which tend to avoid each other in space are classified into the same intrinsic guild. Wilson and Roxburgh (1994) did this by employing a procedure that used one set of point quadrat data to form the guilds and tested this guild classification on an independent set of point quadrats. Wilson and Roxburgh (2001) formed intrinsic guilds from competition experiments, classifying species into guilds to maximise overyield when a species of one guild was grown with one from the other guild. Essentially, the same guild classification resulted from the competition experiments as from the field co-occurrence data. Intrinsic guilds formed by both methods are presumably groups of species that tend to use the same resources. The intrinsic guilds of Wilson and Roxburgh (1994) may be considered the real guilds, i.e., as perceived by the plants. We here test for significant differences between these guilds in functional characters, to make inferences on which niche axes are responsible for the observed niche differentiation between guilds.

Aims

Our aim, therefore, is to use both the limiting-similarity approach and the guild-proportionality approach to test whether the niche axes examined (i.e., light harvesting and mowing resistance) are important for species coexistence in a lawn community. Agreement between the two independent approaches would increase confidence in the conclusions from either alone.

Methods

Study area

The Botany Lawn, University of Otago (Figure 1), 10.2 m × 13.3 m in size, was established in 1968, with only *Agrostis capillaris* and *Festuca rubra* being sown and all other species present within the current community arriving through natural dispersal. The commonest species are the grasses *Holcus lanatus* (Yorkshire fog) and *Agrostis capillaris* (bent), forbs *Trifolium repens* (white clover) and *Hydrocotyle heteromera* (a New Zealand native) and mosses *Eurhynchium praelongum* and *Acrocladium cuspidatum* (Figure 1). Since its establishment, the lawn has been maintained under a consistent regime, being cut to a height of 0.03 m fortnightly in the growing season and monthly in winter, with no application of fertilizer or herbicide and no irrigation (the aver-

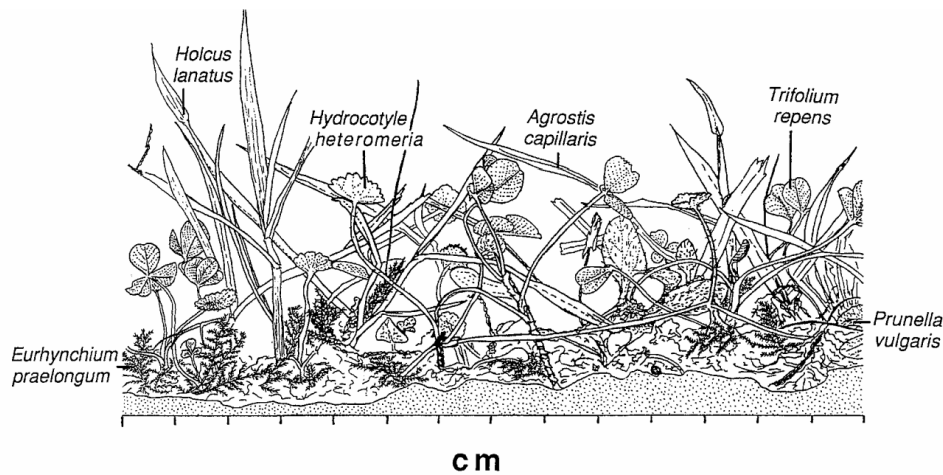


Figure 1. Diagrammatic cross-section through a part of the lawn (from Roxburgh et al. 1993).

age annual rainfall is 812 mm yr^{-1}). This constant and predictable disturbance creates a real community, with opportunity to come to equilibrium – an ideal vegetation system for intensive study. Previous studies have shown that species composition in the lawn is relatively constant over time, and that any variation in species composition was non-directional (Roxburgh and Wilson 2000). This indicates that the species in the lawn community are capable of co-existing.

Sampling methods

Canopy structure. Directly after mowing, seven $0.2 \times 0.2 \times 0.2 \text{ m}^3$ turves were taken from the lawn, placed in a greenhouse to ensure constant growing conditions throughout the study period. They were left for four days to recover before sampling commenced. In sampling, twenty point quadrats were located at regular intervals in each turf, effected by lowering a pin with a sharpened tip ($50 \text{ }\mu\text{m}$ in diameter) vertically into the sward at each point, and recording the species and height of all leaf contacts down to the soil surface. To minimise edge effects, only the central $0.1 \text{ m} \times 0.1 \text{ m}$ of each turf was sampled. Sampling was performed on five dates, each four days apart, to determine if the results were consistent throughout the period between mowing events. This gave a total of 700 points, though a few were bare, and could not be included in the analyses.

Species light-capture characters. Ten leaves of each species were taken from random positions in the turves at the end of the sampling period. Lamina length, width and area were measured using a scanner, and leaf thickness with a micrometer. Lamina fresh mass was taken, and dry mass after oven drying at 80°C . Specific leaf area (SLA , i.e., the lamina area per unit lamina mass) was calculated as:

$$SLA = \frac{A_l}{M_l}$$

where A_l is the area of an individual lamina and M_l is the mass of the lamina.

On completion of point quadratting, above-ground phytomass from the central $0.1 \text{ m} \times 0.1 \text{ m}$ of each turf was harvested, sorted into laminar and non-laminar material for each species, and the results used to calculate lamina mass ratio (L_aMR , i.e., the lamina mass per unit shoot mass) and lamina area ratio (L_aAR , i.e., the lamina area per unit shoot mass):

$$L_aMR = \frac{M_l}{M_s}$$

where M_l is the lamina mass, M_s is the mass of whole shoot and SLA is specific leaf area.

Pigment contents were measured by standard methods: Moran and Porath (1980) and Porra et al. (1989) for Chlorophylls a and b, Lichtenhaler (1987) and Chappelle et al. (1992) for total carotenoid, Reddy et al. (1994) for anthocyanins and UV-B absorbing pigments. A Mowing Removal Index (MRI) value for each species was calculated from the point-quadrat data, as the proportion of its leaf area (i.e., leaf contacts) at the time of measurement that was above the regular mowing height of 0.03 m .

$$MRI_i = \frac{N_{ai}}{N_{ti}}$$

where N_{ai} is the number of leaf contacts of species i and N_{ti} is the total number of leaf contacts for species i .

This gives a measure of alpha-niche for defoliation resistance. A single value of MRI was calculated for each species at each sampling date.

Table 1. The two guilds, with characteristics of the species. Heights of the species are given in Roxburgh et al. (1993).

Guild A			Guild B		
Species	Type	Freq. (%)	Species	Type	Freq. (%)
<i>Agrostis capillaris</i>	G	39.4	<i>Acrocladium cuspidatum</i>	M	0.2
<i>Anthoxanthum odoratum</i>	G	4.6	<i>Eurhynchium praelongum</i>	M	27.3
<i>Bellis perennis</i>	R	5.9	<i>Festuca rubra</i>	G	0.2
<i>Holcus lanatus</i>	G	2.4	<i>Hydrocotyle heteromeria</i>	FN	0.8
<i>Poa pratensis</i>	G	14.0	<i>Hypochaeris radicata</i>	R	6.4
<i>Trifolium dubium</i>	L	14.2	<i>Prunella vulgaris</i>	F	24.9
<i>Trifolium repens</i>	L	2.4	<i>Ranunculus repens</i>	F	4.6

Key: G = Graminoid (Poaceae), R = rosette forb, L = legume (Fabaceae, N-fixer), F = other

forb, M = moss, N = native (other species are exotic); Freq. = frequency

Statistical analyses

Divergence in Mowing Removal Index (MRI) of species co-occurring at a point. Divergence in the Mowing Removal Index of the species co-occurring at a point was compared with random expectation. The test statistic was the variance in MRI among the species present at a point, averaged over all points: a larger variance than expected at random would indicate that the species at a point tend to be different in MRI, demonstrating limiting similarity. Any such assembly rule must be tested against a null model constructed by the Tokeshi principle of including every feature of the observed data except the one it is intended to test (Wilson 1999a). Thus, the null model was constrained so that in the randomised communities each species occurred with the same frequency as in the observed community, while each point contained the same number of leaf contacts as in the observed community. Species occurrences (i.e., leaf contacts) were randomly allocated to points within these constraints using the method of Wilson (1987). The test statistic was calculated for the observed data, and for 2000 randomisations. The mean of those randomisations gave the value expected under the null model. The proportion of randomisations with a test statistic equal to that observed, or more extreme, gave the probability (P) of the observed value of the test statistic under the null model, multiplied by 2 to effect a 2-tailed test.

Divergence in light capture characters of species co-occurring at a point. The randomisation method described above was also used to test for divergence in species light-capture characters, separately for each of the characters measured.

Table 2. Observed and expected variance in Mowing Removal Index (MRI) of species co-occurring at a point in lawn turves at five sampling dates.

Days since mowing	Observed variance	Expected variance	P
4	0.057	0.046	<0.001
8	0.045	0.039	0.012
12	0.045	0.038	0.001
16	0.075	0.067	0.029
20	0.078	0.067	0.009

Exploration of the intrinsic guilds. Differences in MRI and in light capture characters between species in the two intrinsic guilds, the Guild A and Guild B of Wilson and Roxburgh (1994), were examined by t -test, using the species as replicates (Table 1).

Results

Limiting similarity

For all sampling dates, variance in Mowing Removal Index of the species co-occurring at point was significantly greater than expected at random (Table 2). That is, co-occurring species tended to be more different in the proportion of their leaf area held above mowing level than expected at random, i.e., limiting similarity. For example, there would be a tendency at a 2-species point for one of the species to be one with a low MRI and the other to be one with a high MRI. This suggests that differences in response to mowing may be important for species coexistence.

Table 3. Tests for limiting similarity in light capture characters at five sampling dates. SLA = specific leaf area, L_aMR = leaf mass ratio, L_aAR = leaf area ratio, chl_a = chlorophyll *a*, chl_b = chlorophyll *b*, UV = UV absorbing pigments, /dm = per leaf dry mass. n.s. = not significant (*P* values between 0.1 and 0.05 are given for information, but are not interpreted as being significant). Dir = direction, + = co-occurring plants tended to be less similar.

Days since mowing ?	4		8		12		16		20	
Leaf character ?	<i>P</i>	Dir	<i>P</i>	Dir	<i>P</i>	Dir	<i>P</i>	Dir	<i>P</i>	Dir
Width	n.s.		n.s.		n.s.		n.s.		0.020	+
Length:width	0.000	+	n.s.		0.032	+	0.002	+	n.s.	
Thickness	n.s.		n.s.		n.s.		n.s.		n.s.	
Dry mass	0.054		0.060		n.s.		n.s.		0.055	
SLA	n.s.		n.s.		n.s.		n.s.		n.s.	
L_aMR	n.s.		n.s.		n.s.		n.s.		n.s.	
L_aAR	n.s.		n.s.		n.s.		0.092		n.s.	
Chl_a / dm	n.s.		0.001	+	n.s.		n.s.		n.s.	
Chl_b / dm	n.s.		0.037	+	n.s.		n.s.		0.098	
$Chl_a:chl_b$	n.s.		n.s.		n.s.		n.s.		n.s.	
Anthocyanin / dm	0.011	+	0.001	+	n.s.		n.s.		0.072	
UV / dm	n.s.		n.s.		n.s.		n.s.		n.s.	
Carotenoid / dm	n.s.		n.s.		n.s.		n.s.		0.013	+

Table 4. Light capture (leaf) characters for the species in each guild in the lawn, and *P*-values from one-way analyses of variance for differences between guilds. Character abbreviations as in Table 2. n.s. = not significant (i.e., *P* > 0.05, in fact in each case *P* > 0.1).

Leaf character	Mean of the species		<i>P</i>
	Guild A	Guild B	
Leaf width (cm)	0.434	0.340	n.s.
Length:width	14.65	69.48	n.s.
SLA (cm ² /g)	170.1	144.3	n.s.
L_aMR	0.755	0.740	n.s.
L_aAR cm ² /g	138.0	123.0	n.s.
Chl_a / dm (μg/g)	2204	4501	n.s.
Chl_b / dm (μg/g)	650.6	1106.2	n.s.
$Chl_a:chl_b$	3.683	4.106	n.s.
Carotenoid / dm (μg/g)	130.9	233.4	n.s.
UV / dm (μg/g)	199.2	183.8	n.s.
Antocyanin / dm (μg/g)	298.7	323.3	n.s.

Tests for divergence in light-capture characters of the species co-occurring at a point gave 9 significant results (Table 3), all in the direction of greater variance than expected, i.e., the direction expected from the theory of limiting similarity. At 0.05 level of significance, only 3.25 significant results would be expected at random, and the binomial probability of obtaining 17 significant results out of 65 tests is 0.0049 (though this test is approximate because of non-independence of the tests). However, significance at more than one sampling time was seen only

for length:width ratio and anthocyanins. This leaves us with little evidence for limiting similarity in characters that affect light capture but are independent of height.

Differences between intrinsic guilds

The mean Mowing Removal Index of both guilds increased with time after mowing, as the plants grew, but the species of Guild A had an MRI that was at least 20% higher than those of Guild B, and significantly higher, at every sampling date (Figure 2).

Of the light-capture characters measured, the guilds did not differ in any character (Table 4). This provides little evidence for the influence of light competition in community structure, or that niche differentiation in light capture strategy is important for species coexistence in the lawn community.

Discussion

Intrinsic guilds and limiting similarity

Previous work on assembly rules has demonstrated non-random patterns in species distributions, presenting these patterns as evidence for species coexistence via niche differentiation (Wilson 1999a). Many ecologists have been doubtful about the implications of any one pattern, and in most studies the evidence for assembly rules has been weak (Wilson 1999a). We used the intrinsic guilds obtained by Wilson and Roxburgh (1994), which had been formed without any *a priori* assumptions on how the species would fall into guilds, nor any assumption on which characters were relevant to assembly. The

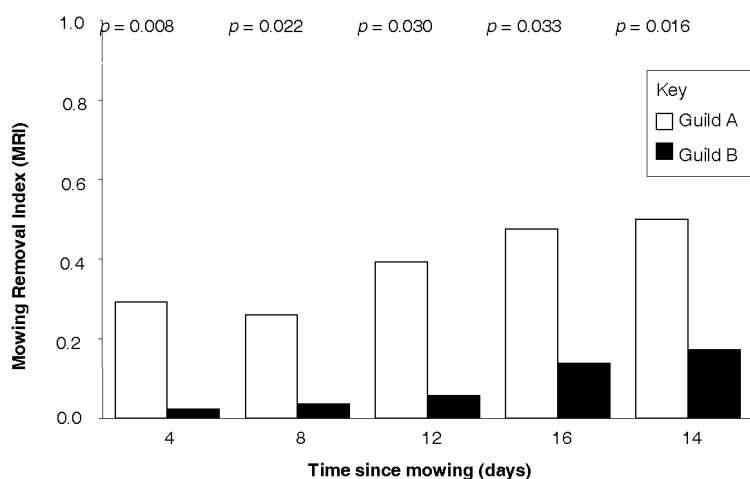


Figure 2. Mean Mowing Removal Index (MRI) of each guild at each sampling date. The P-values are from t-tests for differences between guilds in mean Mowing Removal Index.

intrinsic guilds were simply the guilds that gave the most constant guild proportions in species occurrences (i.e., maximised guild proportionality), formed and tested on independent sets of point quadrats from the Botany Lawn community. Wilson and Roxburgh (2001) gave strong support for this intrinsic guild classification by finding that species in the same intrinsic guild competed more intensely than species from different guilds using a competition experiment. This implied that there was niche differentiation between the guilds (i.e., that the guilds differed in resource use), though it provided no evidence along which niche axis. Our present results show that although the guilds in both the above studies were formed without reference to characters, the guilds differ markedly in MRI. This precisely confirms the result from the limiting-similarity analysis, with a strong limitation to coexistence between species related to their proportion of leaf area removed in mowing. The conclusion is clear: species assembly is constrained so that at any multi-species point there tends to be one (or more) species with a high MRI (i.e., a tall species, that tolerates mowing by regrowth), plus one (or more) species with a low MRI, that avoids mowing through holding most of its leaf area low in the community. MRI is, by definition, a measure of the amount of biomass removed in defoliation. We have demonstrated limitations to coexistence that correlate with MRI. Thus, it appears that differences in strategies for coping with defoliation facilitate species coexistence in this community.

Stratification is often suggested as a mechanism for coexistence in forests (e.g., Nakashizuka 2001), but rarely tested statistically (but see Wilson 1989). Ecologists have sometimes been wary of lawns as ecological communi-

ties, but this lawn has had 35 years to come to equilibrium and it has stratification as complex as many forests, be it on a much finer scale (Roxburgh et al. 1993). In terms of the turnover-rate of the plants/ramets involved, this is vastly longer than any forest has had since environmental change or catastrophic disturbance, from which thousands of years recovery is probably needed for equilibrium to be reached (Kinzig et al. 1999). It is probably relatively longer than in alpine communities, where growth is usually slow. The mowing can be seen as a standardized form of herbivory, and certainly represents a very constant external force. Indeed, Roxburgh and Wilson (2000) found that the species composition of the lawn was relatively constant and that after various types of experimental perturbation, species composition rapidly returned to the pre-perturbation state. It seems likely that the Botany Lawn is close to equilibrium. If assembly rules occur anywhere, they would surely occur here.

Characters and processes

Often, in assembly-rule work, there has been no obvious link of any assembly-rule patterns that have been found to ecological processes. Using characters explicitly chosen to relate to the effect of mowing and to light harvesting strategy, we were able to go beyond simply demonstrating that limiting similarity and guild proportionality were occurring, and link the patterns described to ecological processes. We recognise that multiple characters determine function (Poorter 1999, Press 1999); we used single characters because statistical methods incorporating multiple characters for this purpose are not yet sufficiently developed.

Guild proportionality in the intrinsic guilds of Wilson and Roxburgh (1994) is an assembly rule that has been previously demonstrated on the lawn. Had the guilds been formed and tested on the same data there would be a danger of circularity, but Wilson and Roxburgh were careful to use separate halves of their in-situ lawn data for formation and testing. Even so, it was not known from their work, or that of Wilson and Roxburgh (2001), how the guilds differed ecologically. We have provided strong evidence for differences between the intrinsic guilds and for limiting similarity in MRI (Table 2), and little evidence in light capture characters, except in characters strongly correlated with mowing removal, such as leaf length, area and mass (Table 3). We conclude that the direct effects of defoliation in this community are more important than effects via light competition.

The importance of defoliation for the maintenance of species diversity in plant communities has been known since the pioneering work of Tansley and Adamson (1925). The constant regular mowing of the Botany Lawn is an intense and predictable pressure on the lawn community, and may be expected to have a strong influence on community processes such as competition. Our results indicate that species co-existence is permitted by divergence between species in resistance to this intense and predictable pressure. The dichotomy between tolerance and avoidance strategies for defoliation resistance is well known (Bullock et al. 2001, Cingolani et al. 2005). However, differences in strategy for coping with defoliation cannot themselves explain co-existence. To complete an ecological explanation it would be necessary to establish a link between defoliation and the competitive processes that are assumed to be the basis of limiting similarity and guild proportionality (Wilson 1999a). Species that lose a high proportion of their leaf area to mowing (defoliation tolerators) are likely to depend on rapid rates of nutrient uptake to allow replacement of the foliage that is removed. Species largely avoiding defoliation will not be exposed to this pressure. A certain point may only be able to support a limited number of nutrient-demanding, defoliation tolerators. A defoliation avoider, with lower nutrient requirements, may be better able to co-exist with a defoliation tolerator than another defoliation tolerator. Also, a common consequence of defoliation in grasses and clovers is cessation of root growth and decrease in nutrient uptake (Morvan-Bertrand et al. 1999, Louhahlija et al. 2000). We hypothesize that interspecific differences in response to mowing (i.e., high MRI but mowing tolerance, *versus* low MRI indicating mowing avoidance) could mediate interspecific competition for below-ground resources. If defoliation tolerators (high MRI) cease nutrient uptake after mowing, defoliation avoiders will have a

short period then of less intense competition with them below-ground. Such temporal niche differentiation in below-ground resource use could explain how mowing avoidance can be the basis of species co-existence. We have shown the importance of alpha niche differentiation in species coexistence in this community, but future work needs to be directed towards finding the actual mechanism.

Conclusions

Previously, convincing evidence for assembly rules had been obtained using characters related to reproductive function (e.g., Armbruster *et al.* 1994), but only weak evidence using characters related to vegetative functions. We provide such evidence. The intrinsic guilds were formed from occurrence and competition data, and were here confirmed independently from their characters. The limiting similarity result was obtained from a separate set of occurrence data, and analysed as point-by-point and character-by-character differences, not by guilds. Our study demonstrates that the choice of truly functional characters can lead to valuable hypotheses of the processes that permit species coexistence.

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